# THE ANATOMY AND PHYLOGENETIC POSITION OF *HELICHTHYS*, A REDFIELDIIFORM FISH FROM THE TRIASSIC OF SOUTH AFRICA

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ABSTRACT. The chondrostean redfieldiiform fish *Helichthys*, from the Triassic of Bekker's Kraal, South Africa, is redescribed. The genus is monospecific and five species are synonymized with the type-species *H. browni*. The possible phylogenetic position of the genus within the Redfieldiiformes is discussed.

THE Triassic fish fauna of Bekker's Kraal, South Africa, was first described by Broom (1909) and later by Brough (1931, 1934). I have already redescribed most of the redfieldiiform and perleidiform members of the fauna (Hutchinson 1973) and the palaeoniscoid genus *Dicellopyge* (Hutchinson 1975). This paper includes a redescription of the redfieldiiform genus *Helichthys* and completes my revision of the chondrostean members of the fauna.

The location of specimens cited in this paper is as follows: GN. University Museum of Zoology, Cambridge; NMW. National Museum of Wales, Cardiff (most specimens in these two collections have been recatalogued but retain the prefix P., indicating that they are derived from the D. M. S. Watson collection. The old catalogue numbers prefixed by P. are included to enable identification with references given in earlier publications); SAM, South African Museum, Cape Town.

## THE VALIDITY OF SPECIES PREVIOUSLY INCLUDED IN THE GENUS *HELICHTHYS*

The genus *Helichthys* was erected by Broom (1909) to accommodate three species: *H. browni*, *H. tenuis*, and *H. draperi*. In 1931 Brough removed *H. tenuis* and *H. draperi* to the palaeoniscoid genus *Dicellopyge* and identified six new redfieldiid species, five of which he included in the genus *Helichthys*: *H. elegans*, *H. stegopygae*, *H. obesus*, *H. ctenipteryx*, and *H. grandipennis*. Some new information on the dermal bones of the skull of *H. elegans* was provided by Hutchinson (1973), but in 1975 Jubb and Gardiner cast doubt on the validity of some of the species erected by Brough, and they synonymized *H. stegopygae* and *H. obesus* with *H. browni*.

Brough's descriptions of the five species of *Helichthys* are based on a remarkably small number of specimens: *H. elegans* (3), *H. stegopygae* (1), *H. obesus* (2), *H. ctenipteryx* (1) and *H. grandipennis* (1). All these specimens have been studied in an attempt to assess the validity of the species that they have been claimed to represent.

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*Helichthys elegans* Syntypes NMW. 70. 2G. 96 (P. 13A); NMW. 70. 2G. 97 (P. 13B); GN. 316 (P. 19A). The diagnostic features of this species are, according to Brough (1931, p. 252): a slender body, posteriorly placed dorsal and anal fins, a dorsally flattened head, and a pectoral fin composed of eight stout, largely unjointed rays with fringing fulcra. The presence of most of these features is confirmed here, but there is doubt as to the precise structure of the pectoral fin. The pectoral fin is not preserved in GN. 316, and is only partially present in specimens NMW. 70. 2G. 96 and 70. 2G. 97. In the latter specimens, the posterior edge of the fin is hidden by the body squamation, and fin-ray counts of ten and eight respectively are merely indications of the minimum number of rays present. In both specimens the distal ends of the rays are jointed and bifurcated. All three specimens show that an antopercular, as well as a dermohyal, is present (cf. Brough 1931, text-fig. 5, and Hutchinson 1973, text-fig. 21). How many suborbitals are present is less clear: there appear to be two in NMW. 70. 2G. 96 and one in 70. 2G. 97 (see below). The cheek region in GN. 316 is not sufficiently well preserved to provide information on this point. There is no evidence that the dorso-ventral length of the subopercular is as short as is indicated by Brough (1931, text-fig. 5).

*Helichthys stegopygae*. Holotype NMW. 70. 2G. 83 and 70. 2G. 84 (P. 12D). The diagnostic features of this species are the presence of an antopercular as well as a dermohyal, a single suborbital, and a pectoral fin composed of twenty fine rays which lack fringing fulcra (Brough 1931, p. 254). All but one of these features are clearly present in specimen NMW. 70. 2G. 84, but the anterior edge of the pectoral fin is damaged and it is not possible to confirm or deny the presence of fulcra. The delicate appearance of the pectoral fin-rays is due to the fact that they have been rotated during fossilization and are visible only from an oblique angle.

*Helichthys obesus*. Syntypes NMW. 70. 2G. 83 and 70. 2G. 85 (P. 12B); NMW. 70. 2G. 83 (P. 12C). The diagnostic features of this species are the shortness of the head, the lack of ornament on the dermal skull bones, the absence of an antopercular, the presence of two suborbitals, and a pectoral fin composed of eighteen fine, partially jointed rays (Brough 1931, p. 256). These observations can be checked only against specimens NMW. 70. 2G. 83 and 70. 2G. 85 (the former block contains the body and the latter the head of specimen P. 12B) as the skull and pectoral fin are not preserved in the other specimen. The apparent lack of ornament is explained by the fact that the head of NMW. 70. 2G. 85 is preserved as an impression of the internal surfaces of the dermal bones. An antopercular is present and there appear to be two suborbitals (see below). The pectoral fin is not well preserved and only the proximal ends of about eight rays are visible. The opercular is not articulated with the subopercular and the spatial relationship between these elements indicated by Brough (1931, text-fig. 7) cannot be confirmed.

*Helichthys ctenipteryx*. Holotype NMW. 70. 2G. 85 and 70. 2G. 91 (P. 12A) and counterpart GN. 309 (P. 11A). The diagnostic features of this species are the presence of seven unjointed, unbifurcated rays in the pectoral fin (Brough 1931, p. 258). In specimen GN. 309, in which the pectoral fin is most completely preserved, only the proximal ends of the rays are visible. These are unjointed and unbifurcated, as are

the proximal parts of the rays in other specimens of *Helichthys*, but it is not possible to exclude the possibility that these rays were jointed and bifurcated further distally. The fin-ray count of seven must be considered to represent the minimum number of rays present. As in the case of *H. obesus*, the opercular and subopercular bones are not articulated, and their precise spatial relationships are not clear.

*Helichthys grandipennis*. Holotype NMW. 70. 2G. 86 (P. 14). The diagnostic features of this species are the presence of distally jointed rays in the pectoral fin, and the relatively large size of the pectoral, pelvic, and anal fins (Brough 1931, p. 260). Distal jointing is clearly visible in NMW. 70. 2G. 86, but the relative sizes of the fins are more difficult to establish because the extreme distal parts of the pectoral, pelvic, and anal fins are not preserved. An antopercular is clearly preserved (cf. Brough 1931, text-fig. 10).

From these observations it is clear that the only character that may serve to diagnose separate species of *Helichthys* is the varied condition of the suborbital: the other character-states that were thought to be diagnostic of the species described by Brough are clearly invalid because they are either the result of differing states of preservation (the condition of the pectoral fin-rays), or not as limited in their occurrence as at first appeared (the presence of an antopercular).

In four specimens (NMW. 70. 2G. 84, 70. 2G. 85 (P. 12A), 70. 2G. 85 (P. 12B) and 70. 2G. 96) the suborbital appears to be subdivided, but close inspection reveals that, in the first two specimens mentioned, it is certainly only cracked. There is some doubt as to the condition of the suborbital in NMW. 70. 2G. 85 (P. 12B) and 70. 2G. 96. These specimens may be interpreted in one of three ways: as individuals in which the suborbital is cracked; as forms in which subdivision of the suborbital reflects intraspecific variation; or as representatives of a separate species of *Helichthys*. In view of their poor preservation it does not appear wise to recognize these specimens as constituting a separate species; *H. elegans*, *H. stegopygae*, *H. obesus*, *H. ctenipteryx*, and *H. grandipennis* are therefore regarded as synonyms. This being so, it is clear that all five species should be synonymized with *H. browni* for, as a result of comparisons made between the type specimen of *H. browni* (SAM. 2767) and those of *H. stegopygae* and *H. obesus*, Jubb and Gardiner have already synonymized the two latter species with *H. browni* (1975, p. 415).

## SYSTEMATIC DESCRIPTION

Subclass CHONDROSTEI
Order REDFIELDIIFORMES
Family *incertae sedis*
HELICHTHYS Broom, 1909

1909 *Helichthys* Broom, p. 254
1931 *Helichthys* Broom; Brough, p. 246
1973 *Helichthys* Broom; Hutchinson, p. 274

*Emended diagnosis*. Redfieldiiform fish in which the dermosphenotic is equal in size to the dermopterotic and in which an antopercular is present. Premaxilla probably absent. Two pairs of parietals present, the

anterior pair being roughly quadrangular and the posterior pair roughly triangular. Dermopterotic narrow posteriorly. Lower jaw deep posteriorly and tapering to a point at the symphysis. Suborbital triangular with rounded corners. Pectoral girdle massive.

*Type (and only) Species. Helichthys browni* Broom.

*Helichthys browni* Broom

1909 *Helichthys browni* Broom, pp. 254–257; pl. 12, fig. 7.
1931 *Helichthys elegans* Brough, pp. 248–252; text-figs. 4–5, pl. 2, figs. 1–2.
1931 *Helichthys stegopygae* Brough, pp. 252–254; text-fig. 6, pl. 2, fig. 3.
1931 *Helichthys obesus* Brough, pp. 254–256; text-fig. 7, pl. 2, fig. 3; pl. 3, fig. 1.
1931 *Helichthys ctenipteryx* Brough, pp. 256–259; text-figs. 8–9, pl. 3, fig. 2.
1931 *Helichthys grandipennis* Brough, pp. 259–261; text-fig. 10, pl. 3, fig. 3.
1973 *Helichthys elegans* Brough: Hutchinson, pp. 275–277; text-figs. 21–22.

*Horizon and locality.* Lower Cynognathus Zone (Scythian) of the Karroo Series at Bekker's Kraal, Rouxville, Orange Free State, South Africa.

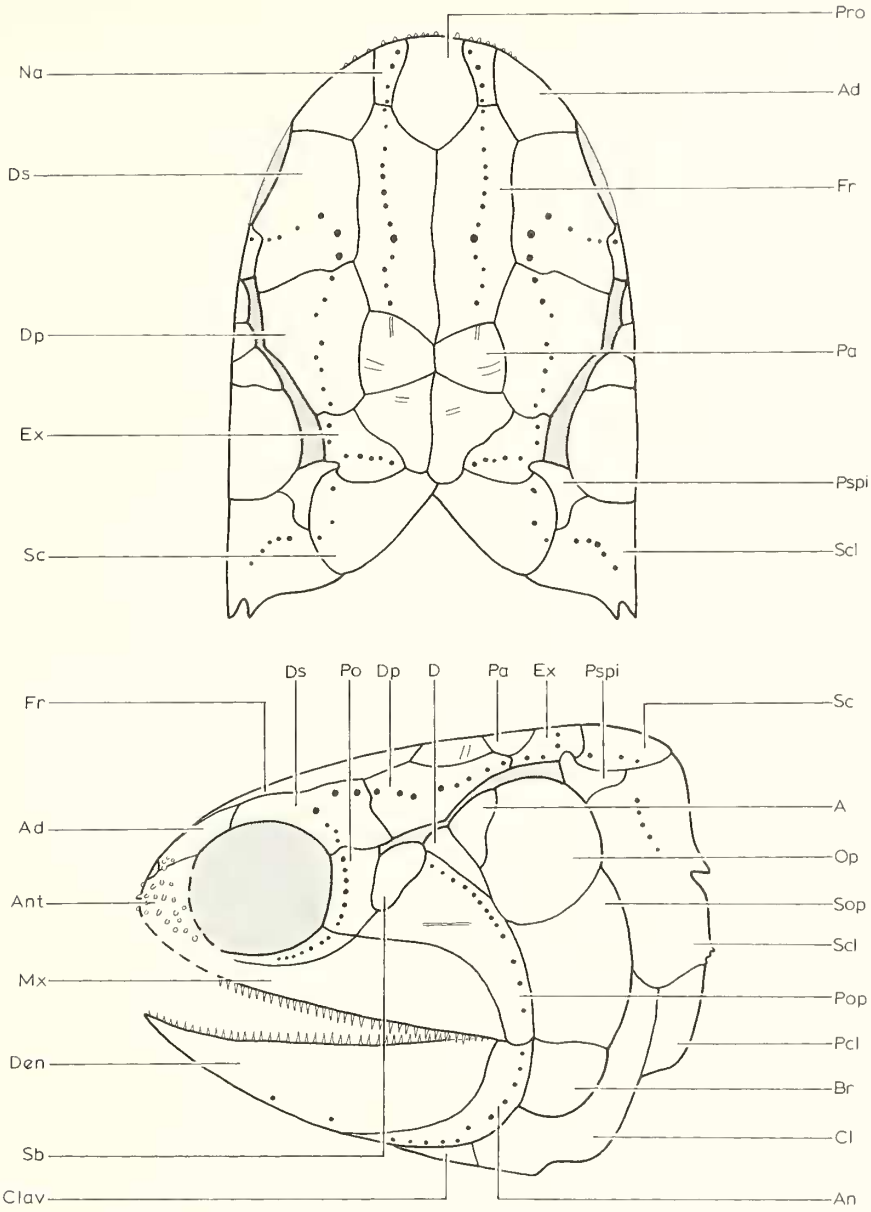
*Diagnosis.* As for the genus *Helichthys.*

*Holotype.* SAM. 2767 (Broom 1909, pl. 12, fig. 7).

*Material.* NMW. 70. 2G. 83 and 70. 2G. 85 (P. 12B); 70. 2G. 83 (P. 12C, text-fig. 3) (Brough 1931, pl. 2, fig. 3; pl. 3, fig. 1; text-fig. 3); 70. 2G. 83 and 70. 2G. 84 (P. 12D) (Brough 1931, pl. 2, fig. 3); 70. 2G. 85 and 70. 2G. 91 (P. 12A) (Brough 1931, pl. 3, fig. 2) and counterpart GN. 309 (P. 11A); 70. 2G. 86 (P. 14) (Brough 1931, pl. 3, fig. 3); 70. 2G. 96 (P. 13A) (Brough 1931, pl. 2, figs. 1–2); 70. 2G. 97 (P. 13B) (text-fig. 2); GN. 316 (P. 19A) (Hutchinson 1973, text-fig. 22); GN. 320 (P. 25); GN. 325 (P. 29B); and GN. 350 (P. 53).

*Description. H. browni* is a fusiform fish attaining a maximum length of about 107 mm (NMW. 70. 2G. 97) measured from the snout tip to the posterior tip of the body lobe; the antero-posterior length of the skull is equal to just under 20% of this distance. The skull is short and in dorsal view appears broad and blunt-snouted.

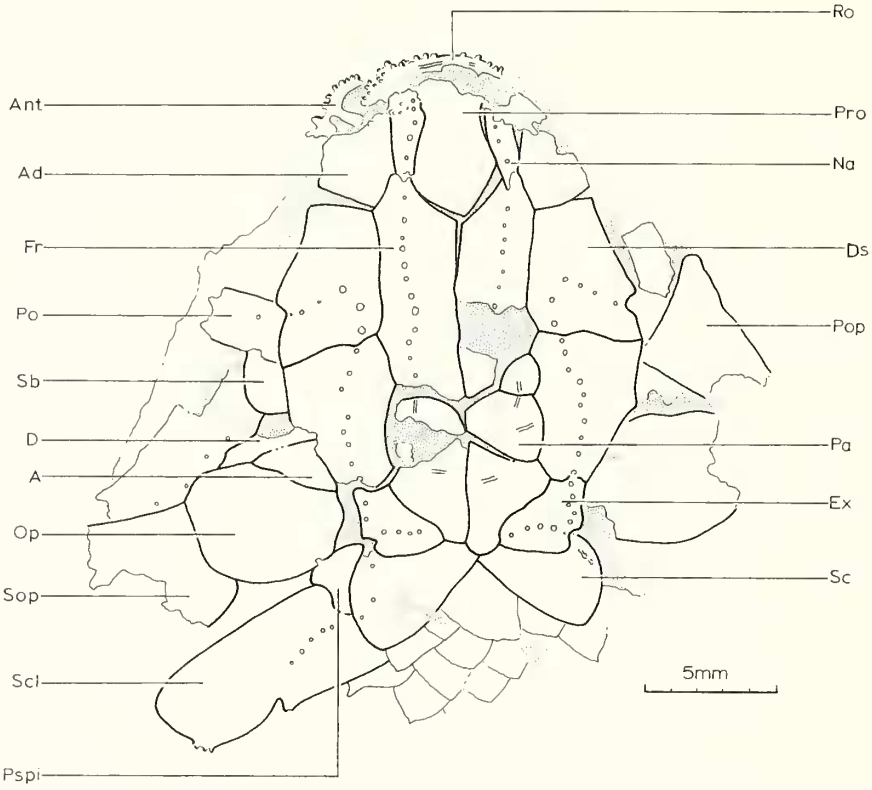
*Skull.* To enable easy comparison of *Helichthys* with other recently described redfieldiiform genera, the names of the dermal bones of the skull used by Schaeffer (1967), Schaeffer and Mangus (1970) and Hutchinson (1973) have been adopted here. It is likely, however, that work on the comparative anatomy of the chondrostean skull at present being undertaken will reveal homologies that will necessitate the renaming of bones, particularly of those forming the lateral part of the skull roof. The restoration of the skull (text-fig. 1) is based on information derived from several specimens of which GN. 316 (Hutchinson 1973, text-fig. 22) and NMW. 70. 2G. 97 (text-fig. 2) have yielded the most complete details. It differs in several important respects from previously published restorations (e.g. Brough 1931, text-fig. 5, and Hutchinson 1973, text-fig. 21), notably in the dorsal region of the cheek. The frontal is roughly rectangular, and lies directly anterior to the parietal elements. The supraorbital sensory canal is clearly visible as it opens to the exterior via a single row of large, well-defined pores, each of which is circumscribed by a ridge. These pores vary in size, and are especially large midway along the frontal. The supraorbital canal extends posteriorly to the posterior edge of the frontal, but continues on to the anterior parietal as a pit-line. There are two pairs of parietals, but in specimen NMW. 70. 2G. 97 (text-fig. 2) the anterior parietal of the right side of the skull has fragmented and consists of two elements. The fact that such fragmentation has only occurred on one side of the skull makes it extremely unlikely that the presence of




TEXT-FIG. 1. *Helichthys browni* Broom. Restoration of skull and pectoral girdle in dorsal and lateral view, × 3·5 approx.

a third parietal is a character of taxonomic significance; it is here regarded as an intraspecific variation. The dermopterotic and dermosphenotic are broad and contribute to the extreme lateral breadth of the skull roof.

The opercular apparatus is similar in shape to that of *Cionichthys dunklei* (Schaeffer 1967, text-fig. 6) and is composed of an almost circular opercular, a subopercular and a single branchiostegal ray. A large, triangular antopercular occurs at the anterodorsal corner of the opercular. The presence of an antopercular has been regarded as a diagnostic character of the Brookvaliidae (Hutchinson 1973, p. 322) and its undoubted presence in *H. browni*, which otherwise displays character states expected in a member of the Redfieldiidae, indicates that the classification of the Redfieldiiformes is not as clear-cut as has been previously suggested by the present author (1973). The possible phylogenetic position of *Helichthys* is discussed below.




TEXT-FIG. 2. *Helichthys browni* Broom. Dorsal view of skull of specimen NMW. 70. 2G. 97 (P. 13B).

A dermohyal lies wedged between the antopercular and the posterodorsal edge of the preopercular. The preopercular bears a horizontal pit-line (NMW. 70. 2G. 86) as well as the usual sensory canal. The suborbital is roughly triangular, but has rounded corners.

The structure of the snout is incompletely known and little can be added to the description of that part of the anatomy of *Helichthys* given by me in 1973 (p. 276).

The anterior ends of the nasal, the antorbital, and rostral bones are ornamented with tubercles. The postrostral does not bear ornament. No evidence of a premaxilla was found in any specimen, and it is assumed to be absent. The lower jaw is deep posteriorly, the angular being particularly massive, and tapers sharply towards the symphysis. The dentition is composed of a row of pointed teeth that lies medial to a zone of smaller, less regularly spaced teeth (NMW. 70. 2G. 96).

*Pectoral girdle.* The pectoral girdle is massive. The supracleithrum is broad antero-posteriorly and its posterior edge is notched at the point where the infraorbital sensory canal passes on to the body squamation. There is a postspiracular bone at the antero-dorsal corner of the supracleithrum, the antero-dorsal corner of which fits into a notch in the postero-ventral corner of the extrascapular (NMW. 70. 2G. 97, text-fig. 2).

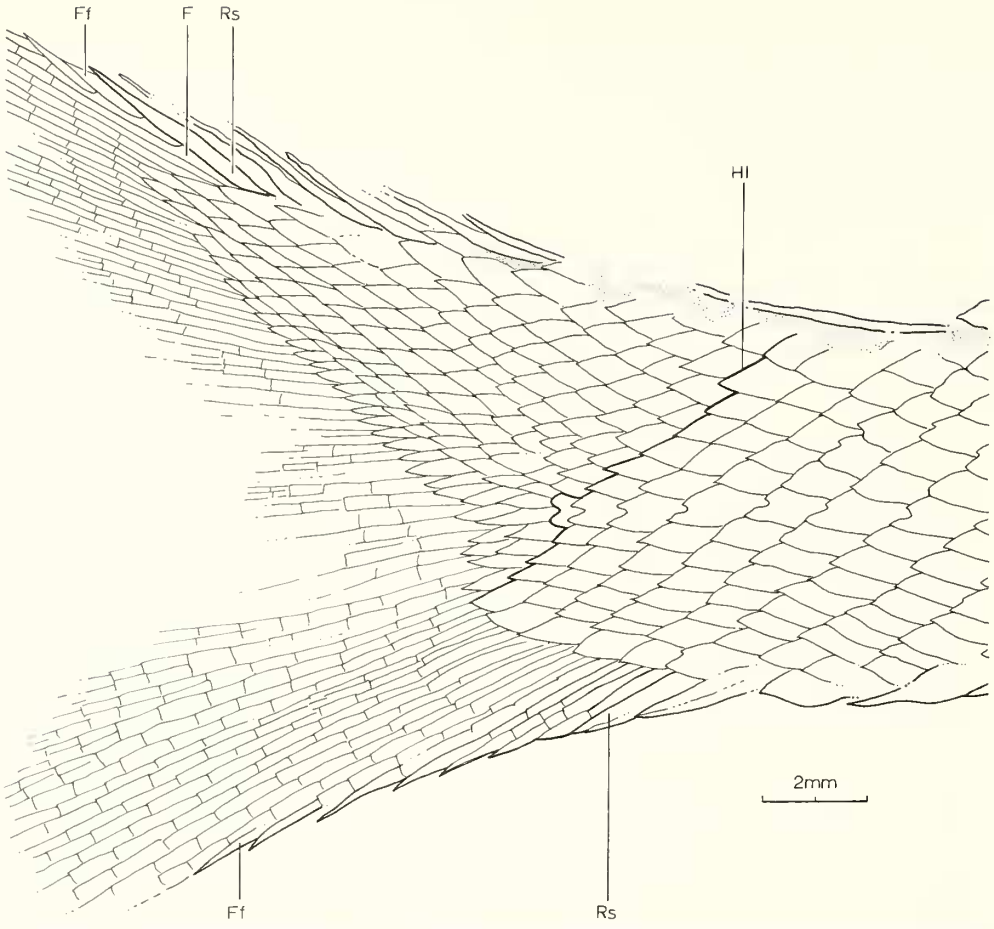
*Paired fins.* The fin-rays of the pectoral and pelvic fins bifurcate distally and bear fringing fulcra. Jointing is even throughout the length of the pelvic fin-rays but limited to the distal ends of the rays in the pectoral fin. There are at least twenty rays in the pectoral fin (NMW. 70. 2G. 84) and at least thirteen in the pelvic fin (NMW. 70. 2G. 91).

*Unpaired fins.* The dorsal and anal fins are similar in shape and size, and are situated fairly close to the tail although the dorsal fin is slightly more anterior in position than the anal fin. In both fins the rays are evenly jointed, bifurcate distally, and bear fringing fulcra. The dorsal fin is composed of at least twenty-four rays (NMW. 70. 2G. 83, P. 12c) and the anal fin of twenty-three rays (NMW. 70. 2G. 86).

The best-preserved caudal fin is seen in specimen NMW. 70. 2G. 83 (text-fig. 3) in which, unfortunately, the skull is not preserved. That this specimen is *H. browni* is, however, confirmed by the fact that all the anatomical features of the caudal fin described below are seen also in NMW. 70. 2G. 96 (P. 13a), a specimen with an almost perfectly preserved skull and an undoubted member of the species.

The caudal fin is hemiheterocercal and equilobate. The angle between the axis of the body and the axis of the body lobe is about 35°. A hinge line is present but is not very conspicuous because the anterior scales of the body lobe and the posterior scales of the body are similar in size and shape. The flank scales through which the lateral line passes each bear a marked indentation in their posterior borders and are clearly differentiated from the other body scales. The lateral line does not appear to cross the hinge line. Most of the body lobe scales form a regular pattern with their long axes orientated in a postero-dorsal direction, the exceptions being the scales that border the postero-ventral edge of the body lobe; these are slender and orientated with their long axes directed along the axes of the rays with which they are associated.

The caudal web is composed of 64 rays: 18 in the ventral lobe and 46 in the dorsal lobe. The five or six rays that form the dorsal edge of the caudal web are epaxial in position; of these, three are associated with scales of the body lobe, and the proximal ends of two or three are fused to the posterior caudal ridge scale. The caudal fin-rays are evenly jointed and bifurcate close to their distal ends; those forming the leading edges of the fin web bear fringing fulcra.




TEXT-FIG. 3. *Helichthys browni* Broom. Right side of caudal fin of specimen NMW. 2G. 83 (P. 12c).

*Squamation.* The scale formula of *H. browni* is difficult to determine precisely but appears to be:

$\frac{29}{9\ 22\ 35}$ 42. The scales do not bear an ornament except in the case of a few large flank scales on which low ridges are just visible. The scales of the anterior flank region are rhombic and bear up to five or six pectinations on their posterior edges. Further posteriorly the scales become leaf-shaped and bear either one or two pectinations or have smooth posterior edges. The scales through which the lateral line passes differ from the other body scales in having an indentation in their posterior edges.

## THE PHYLOGENETIC POSITION OF *HELICHTHYS*

The order Redfieldiiformes has most recently been diagnosed by Hutchinson (1973, p. 238) but, although including characters apomorphous within the Chondrostei, only one may safely be regarded as an autapomorphous character justifying the

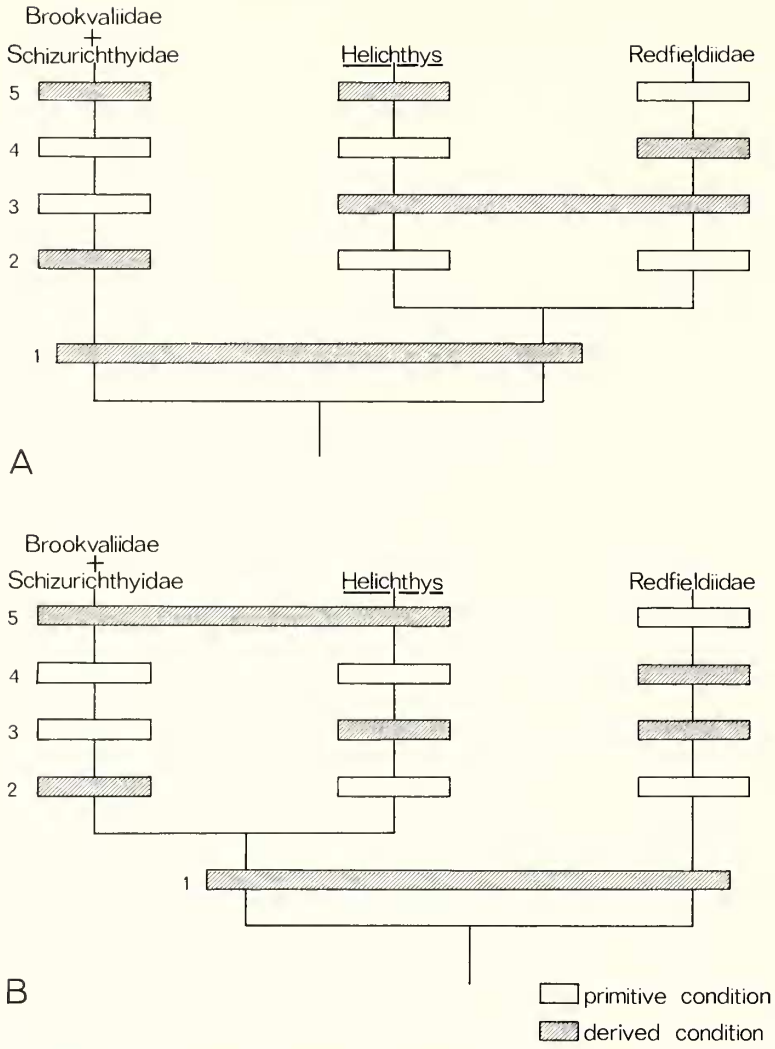
recognition of the Redfieldiiformes as a monophyletic group. This character is seen in the structure of the snout, which is composed of an antorbital that forms an extensive part of the anterior orbital edge and borders the single narial opening. Other character states that are not found in all members of the Redfieldiiformes, but which may reasonably be expected to be found in the redfieldiiform ancestral morphotype are: the presence of a dermosphenotic and a single adnasal which together border the dorsal orbital edge; and the presence of a single branchiostegal ray. The identification of all these character states in *Helichthys* leaves no doubt that the genus is a member of the Redfieldiiformes.

Within the Redfieldiiformes it is possible to identify two clear monophyletic groups; the Brookvaliidae together with the Schizurichthyidae, and the Redfieldiidae. These families have been diagnosed by Hutchinson (1973, pp. 239, 285, and 271). Again, these diagnoses contain a mixture of plesiomorphous and apomorphous character states. The autapomorphous characters that enable recognition of two monophyletic groups within the Redfieldiiformes are as follows: Brookvaliidae plus Schizurichthyidae, the presence of a crescent-shaped dermosphenotic; Redfieldiidae, the absence of premaxillary and antopercular elements. Consideration of just these, and one other character state (the shape and number of parietal elements), can be expressed in the cladogram (text-fig. 4A) which demonstrates that *Helichthys* cannot be included in either of the two monophyletic groups noted above. It also implies that the Brookvaliidae plus Schizurichthyidae are the sister-group of *Helichthys* and the Redfieldiidae combined.

There is one reason, however, for doubting the validity of this cladogram: it implies that two pairs of parietals, such as are seen in *Helichthys*, evolved independently in the phylogenetic line leading to the monophyletic group Brookvaliidae plus Schizurichthyidae. The parietals of *Helichthys* are quite distinctive: the anterior element bears two pit-lines and is roughly quadrangular; the posterior element is roughly triangular and bears the posterior pit-line. Paired parietals of almost identical shape are seen in all members of the Brookvaliidae in which this part of the skull roof is well preserved i.e. in *Ischnolepis*, *Brookvalia*, and *Phlyctaenichthys* (*Atopocephala*, in spite of the restoration given by Hutchinson 1973, text-fig. 7, is a poorly preserved unique specimen and the possibility of its having four parietals cannot be discounted). Significantly, two pairs of parietals never occur in members of the Redfieldiidae, although there is considerable variation of parietal structure within the group. It is legitimate, therefore, to regard the two pairs of parietals as evidence of close relationship between *Helichthys* and the Brookvaliidae plus Schizurichthyidae, a relationship illustrated in text-fig. 4B.

Once again, it is clear that *Helichthys* is not a member of either of the two monophyletic groups that constitute the rest of the Redfieldiiformes, but it does demonstrate that the Brookvaliidae plus Schizurichthyidae combined with *Helichthys* could be regarded as the sister-group of the Redfieldiidae.

There is a third hypothesis concerning the phylogenetic position of *Helichthys*; that it constitutes the sister-group of all other redfieldiiforms. This hypothesis can be dismissed at present because there are no known apomorphic characters common to all members of the Brookvaliidae, Schizurichthyidae, and Redfieldiidae that are not found in *Helichthys*.




TEXT-FIG. 4. Cladograms expressing alternative phylogenetic positions of *Helichthys* within the Redfieldiiformes. A. Assumes independent evolution of two pairs of parietals in separate phylogenetic lines; B. assumes independent loss of premaxillae in separate phylogenetic lines. Key to character states considered: (1) structure of antorbital; (2) crescent-shaped dermosphenotic; (3) loss of premaxillae; (4) loss of antopercular; and (5) presence of two pairs of parietals.

It is clear from the above discussion that it is not at present possible to define the phylogenetic position of *Helichthys* within the Redfieldiiformes with any degree of certainty. This conclusion is, perhaps, not surprising and is due to a number of factors. Preservation of fossil material is rarely perfect and is anyway limited to hard parts of the anatomy. (If, for example, one could be certain that *Helichthys* lacked a premaxilla, the cladogram in text-fig. 4A could be regarded with more confidence.)

Secondly, a minimum number of character states have been considered in the above analysis. If all known redfieldiiform synapomorphies had been taken into account it might have been possible to construct cladograms that would allow choices involving greater degrees of confidence to be made. Such an exercise is beyond the scope of this paper.

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Dr. Peter Hutchinson died on 5th August 1977 after a brief illness; offprints of this article can be obtained from Dr. C. M. Patterson, Department of Palaeontology, British Museum (Natural History).